

Age at first breeding of the African Penguin

Philip Whittington¹, Norbert Klages², Robert Crawford³, Anton Wolvaardt⁴ and Jessica Kemper⁵

¹Avian Demography Unit, Department of Statistical Sciences, University of Cape Town, Rondebosch 7701, South Africa

²Institute for Environmental and Coastal Services, Nelson Mandela Metropolitan University, PO Box 77000, Port Elizabeth, 6031, South Africa

³Marine and Coastal Management, Private Bag X2, Roggebaai 8012, South Africa

⁴Western Cape Nature Conservation Board, Private Bag X5014, Stellenbosch 7599, South Africa

⁵Ministry of Fisheries and Marine Resources, PO Box 394, Lüderitz, Namibia

*Corresponding author, e-mail: Philip.Whittington@nmu.ac.za

Re-sightings of African Penguins *Spheniscus demersus* flipper-banded as chicks were used to estimate the age of first breeding. Data from five breeding colonies in three regions were analysed: Ichaboe and Mercury islands, Namibia; Dassen and Robben islands, Western Cape and Bird Island, Algoa Bay, Eastern Cape, South Africa. Between 6% and 9% of chicks banded at each colony were subsequently recorded breeding. The average age at first breeding was 4–6 years (range 2–8 years). Oiling, and the subsequent cleaning and rehabilitation procedures, did not affect the age of first breeding. Mean age at first recorded breeding differed between cohorts at the same colony by up to 2.4 years and between colonies by up to 1.1 years. It averaged later at Mercury Island (6 years) than at the other four colonies (5 years). Penguins from colonies in the Western Cape of South Africa, where penguin numbers are generally increasing, bred at a significantly younger age than at colonies in the Eastern Cape and Namibia. However, re-sighting effort was not uniform among colonies or between years and probably affected differences between cohorts and colonies.

Introduction

The African Penguin *Spheniscus demersus* is endemic to southern Africa, breeding at 29 localities in Namibia and South Africa. The population decreased by 90% during the 20th century and the species is considered 'Vulnerable' under the IUCN Red Data list criteria (Crawford 1998, BirdLife International 2000, Whittington *et al.* 2000a, BirdLife International 2004). There is a paucity of robust demographic parameters for the African Penguin at different colonies and in different regions (Whittington *et al.* 2000a). Previous studies estimated age at first breeding of African Penguins in South Africa to be 3–5 years at St Croix Island, Algoa Bay, (Randall 1983), 2–5 years at Stony Point, (JH Hofmeyr *in litt.*), 3–7 years at Boulders (Crawford *et al.* 2000) and 4–5 years at Robben Island, Western Cape (Crawford *et al.* 1999). Age at first breeding is well documented for nine of the world's 17 species of penguins but for only one, the Magellanic Penguin *S. magellanicus*, in the genus *Spheniscus*. This paper compares the age of first recorded breeding of African Penguins of known age at five colonies within three different regions. Comparisons are made between different cohorts at each colony, between different colonies within regions, between regions and between birds that had been oiled, cleaned and released and those that had never been oiled. Mean age at first breeding is further compared with those values derived for other penguin species.

Methods

The age at which the penguins first made breeding attempts was estimated from data held by the Avian Demography

Unit, based on re-sightings of birds banded as chicks. The distribution of penguin colonies around the coast forms three main clusters and these were used as the regions in the analysis. Namibian colonies are separated from those in the Western Cape of South Africa by 600km and there is a gap of another 600km between Western Cape colonies and those in Algoa Bay in the Eastern Cape. Data were analysed from five colonies: Bird Island; Robben and Dassen islands in the Western Cape and Ichaboe and Mercury islands in Namibia. Penguin chicks at Bird Island were banded by staff of the Port Elizabeth Museum, those at Robben and Dassen islands by staff of Marine and Coastal Management (MCM) and those in Namibia by staff of the Namibian Ministry of Fisheries and Marine Resources and by staff of MCM. Most of the re-sighting data from Bird Island were collected by NTWK and staff of the Port Elizabeth Museum and were available from 1992 until the end of May 2001. MCM and PAW contributed additional sightings from annual census visits made between 1991 and 1999. Thorough searches of the penguin colony on Robben Island were made on a quarterly basis from 1995 to 1999 by PAW. Staff of MCM contributed additional sightings in one section of the colony on a fortnightly basis and in the whole colony during the annual census of breeding African Penguins. Staff of the Western Cape Nature Conservation Board at Dassen Island made sightings of banded penguins on an almost daily basis from August 1994 to June 1999. Two areas of the island received intensive fieldwork during an investigation into the growth of chicks, while these areas and two further areas were part of a study where a sample of nesting burrows was

checked for occupancy on a weekly basis. Staff of MCM collected additional information during the annual nest count. The few re-sightings received from Dassen Island prior to 1994 were not computerised and not used in this analysis. In Namibia, re-sightings of African Penguins for the years 1990 to the end of June 2001 at Ichaboe Island and to February 2001 at Mercury Island were received from staff of the Namibian Ministry of Fisheries and Marine Resources. Re-sighting effort at these two colonies was fairly consistent throughout the study period, and special efforts were made to record banded birds on a fortnightly basis, coupled with observations made on daily patrols of the islands.

The database was investigated for all records of breeding by birds banded as chicks between 1992 and 1995. Breeding was defined as incubation of eggs or guarding of chicks. No attempt was made to monitor the success or failure of breeding attempts. The age of each bird on the first apparent occurrence of breeding was computed in days as the period elapsed between date of banding and date of re-sighting, and then divided by 365 to obtain the value in years. Chicks were usually banded about two months after hatching.

Trends were compared between different cohorts for each colony and between different colonies. Mean and median ages of first breeding were computed for each cohort at each colony. One-way ANOVA tests were performed on data for the five colonies. Comparisons between means of the age of first recorded breeding were made between colonies for each cohort and between cohorts for each colony. Data from Robben and Dassen islands and from Ichaboe and Mercury islands were pooled to compare means between the three regions (Eastern Cape, Western Cape and Namibia). Data for birds that had been restored to the breeding population after being oiled were compared with those for non-rehabilitated birds. Due to

the difficulty of accurately sexing African Penguins in the field, no comparison was possible between the ages of first recorded breeding of males and females.

An attempt was made to estimate the monitoring effort at each colony by plotting the number of days in each year when observations were made, along with the total number of re-sightings of banded penguins (including non-breeding birds) made in that year. This assessment of monitoring effort was restricted to re-sightings of birds banded as chicks in the years covered by the analysis. The number of observation days alone could include a large number of days when relatively few birds were re-sighted, thereby inflating the monitoring effort. However, by considering re-sightings alone, the same effect could result from a few days of monitoring on which many re-sightings were made.

Results

The numbers of African Penguins banded as chicks at each of the study colonies between 1992 and 1995 varied considerably between years and between colonies. A total of 6 839 were banded, of which 473 were subsequently recorded breeding (Table 1). Estimates of age at first breeding ranged from 2.1–8.7 years, with mean age at first breeding varying from 3.8 to 6.2 years (Table 2) and median age from 3.8 to 6.4 years (Table 3).

Differences between cohorts

The numbers of birds recorded breeding from each of the cohorts varied between two and 83 (Table 1). Age at first recorded breeding of African Penguins that were banded as chicks at Bird Island differed for all three cohorts (Appendix 1). Most of those banded in 1992 were not recorded breeding until five years of age or older. All but one of those banded in 1994 were over four years old when first found

Table 1: Numbers of African Penguins banded as chicks between 1990 and 1995 (Nba), and the numbers (NBr) and proportion (%Br) that were subsequently recorded breeding at each of five breeding colonies

Breeding colony	1992			1993			1994			1995			Total		
	Nba	NBr	%Br	Nba	NBr	%Br	Nba	NBr	%Br	Nba	NBr	%Br	Nba	NBr	%Br
Bird Island	66	14	21	1	0	0	495	36	7	574	53	9	1 136	103	9
Robben Island	660	59	9	394	26	7	53	2	4	0	0	–	1 107	87	8
Dassen Island	1 062	83	8	510	26	5	399	5	1	0	0	–	1 971	114	6
Ichaboe Island	411	25	6	537	16	3	112	12	11	211	21	10	1 271	74	6
Mercury Island	785	55	7	422	32	8	111	6	5	36	2	6	1 354	95	7
Total	2 984	236	8	1 864	100	5	1 170	61	5	821	76	9	6 839	473	7

Table 2: Mean age at first recorded breeding (in years) for African Penguins banded as chicks at five breeding colonies

Breeding colony	Year banded				All years
	1992	1993	1994	1995	
Bird Island	6.0	–	5.5	4.8	5.2
Robben Island	4.8	4.9	3.8	–	4.8
Dassen Island	4.6	4.7	4.4	–	4.6
Ichaboe Island	5.6	5.6	4.6	4.8	5.3
Mercury Island	6.2	5.2	5.2	3.8	5.7
Rehabilitees	5.0	5.6	–	5.2	5.1

Table 3: Median age at first recorded breeding in years for African Penguins banded as chicks at five breeding colonies

Breeding colony	Year banded				All years
	1992	1993	1994	1995	
Bird Island	6.4	–	5.1	4.8	5.2
Robben Island	4.9	4.8	3.8	–	4.9
Dassen Island	4.2	4.8	4.4	–	4.3
Ichaboe Island	5.4	5.4	4.7	4.7	5.1
Mercury Island	6.0	5.3	5.3	3.8	5.8
Rehabilitees	4.6	5.6	–	5.2	5.2

breeding, most being in their fifth year. For birds banded at Bird Island in 1995, the maximum possible age at first breeding was six years, because 2001 was the last year for which observations were available. Of the 52 birds in this 1995 cohort that were recorded breeding, 47% were in their sixth year and all but one of the remaining birds were in their fourth or fifth year of life.

The majority of first breeding attempts by Robben Island and Dassen Island cohorts were detected when the birds were between three and five years old (Appendix 1).

At Ichaboe Island in Namibia, birds banded in the years 1992 to 1995 showed a similar pattern of age at first recorded breeding (Appendix 1). With the exception of birds banded in 1993, most of which were not detected breeding until their sixth or seventh year, the majority were first recorded breeding in their fifth or sixth years of life.

Age at first recorded breeding seemed to show most variation at Mercury Island (Appendix 1). Sixteen (29%) of those banded in 1992 were first recorded breeding in their sixth year, while 17 (31%) were not recorded breeding until they were over seven years old. Most birds banded in 1993 at Mercury Island were in their sixth year or younger when first discovered breeding but many were not found breeding until their seventh year (Appendix 1).

At Robben Island, mean ages of first recorded breeding did not differ significantly for the 1992–1994 cohorts ($F_{2,84} = 0.76$, $P = 0.39$). For Dassen Island, a similar result was obtained for these cohorts ($F_{2,111} = 0.25$, $P = 0.78$). For Ichaboe Island, mean ages at first recorded breeding differed significantly for all but the 1992 and 1993 cohorts. ANOVA tests on all cohort pairings for both Bird Island and Mercury Island showed highly significant differences between the means of age at first recorded breeding ($P < 0.01$ in all cases).

Differences between colonies

The majority of African Penguins at Bird, Robben and Dassen islands were first recorded breeding between their fourth and sixth years of life (between three and five years old) (Figure 1). At Ichaboe and Mercury islands, most were first recorded breeding between their fifth and seventh years.

Mean and median ages of first recorded breeding at Robben and Dassen islands differed by 0.2 years (mean) and by a maximum of 0.7 years (median) for the 1992 and 1993 cohorts (Tables 2 and 3). The 1994 cohorts differed by 0.6 years for both mean and median ages but the sample sizes were only two and five respectively. For the 1992 cohort, mean and median ages of first recorded breeding for birds banded at the two Namibian colonies and at Bird Island were greater than for the two Western Cape colonies. Bird Island recorded the highest median age of first recorded breeding for that cohort. Values for the 1993 cohort were greater at the two Namibian colonies than at those in the Western Cape. Only Bird and Ichaboe islands had sample sizes of over 10 birds that were re-sighted breeding for the 1994 and 1995 cohorts (Table 1). Bird and Mercury islands had the highest mean and median ages of first recorded breeding for birds banded in 1994, Robben Island having the lowest. Birds banded in 1995 at Bird and Ichaboe islands had similar mean and median values.

When data for all cohorts were combined, the mean and

median ages at first recorded breeding were between four and five years old for Robben and Dassen islands and between five and six years old for the other three colonies (Tables 2 and 3). Mercury Island birds had the greatest mean age at first recorded breeding and averaged six months later than birds at Ichaboe and Bird islands (Tables 2 and 3). The mean ages of first recorded breeding differed significantly for all colonies, with the exception of Robben and Dassen islands ($F_{1,199} = 1.1$, $P = 0.3$). Ichaboe and Mercury islands were statistically significantly different from the other three colonies and from each other. Using data for birds banded in 1992, which was the only banding year for which reasonable numbers of birds from all five colonies were recorded breeding, the mean ages of first recorded breeding were found to differ for all five colonies. Excluding data from Bird Island, which showed the largest variance, made little difference to the result ($F_{3,218} = 24.58$, $P < 0.01$).

Differences between regions

Means of the data from Bird Island and the two Namibian islands combined did not differ significantly from each other ($F_{1,270} = 3.48$, $P = 0.06$), but were statistically significantly different from the combined data of the two Western Cape islands ($F_{2,470} = 21.97$, $P < 0.01$).

Differences between rehabilitated and non-rehabilitated birds

Only five penguins that had been banded as chicks between 1992 and 1995 and then subsequently oiled and rehabilitated were found breeding (Table 4). They comprised one bird from Bird Island, three birds from Robben Island and one from Dassen Island. Their first recorded ages of breeding ranged from 4.1 to 6.1 years old (Figure 2). The mean age of first recorded breeding for these five birds was 5.1 years (Table 2) and the median age was 5.2 years (Table 3).

Mean age at first recorded breeding of the rehabilitated birds did not differ significantly from that recorded at Robben and Dassen islands, using data for all years combined ($F_{2,203} = 0.99$, $P = 0.37$). All but one of the rehabilitated birds that were recorded breeding had been banded at one of these two colonies.

Re-sighting effort

Re-sighting effort of banded African Penguins at Bird Island intensified from about 1995. Monitoring effort at this colony, in terms of the number of days when re-sightings were made and of the total number of re-sightings made per year, was high in 1994, 1995 and 1999 (Figure 3a). At Robben and Dassen islands, monitoring effort became more regular and intensified from 1994 onwards (Figure 3b and c). Re-sighting effort from the Namibian islands was complicated by the fact that data were missing for certain periods. Only six months of data were available for the years 1995, 1996, 1997 and 1998 from Ichaboe Island and for 1994, 1995, 1997 and 1998 from Mercury Island. However, proportions of birds banded as chicks that were subsequently found breeding on these islands tended to be similar to the other three colonies (Table 1). At Ichaboe Island there was a peak in re-sighting effort in 1993 (Figure 3d). Re-sighting effort at Mercury Island peaked in 1992 and 1996 (Figure 3e).

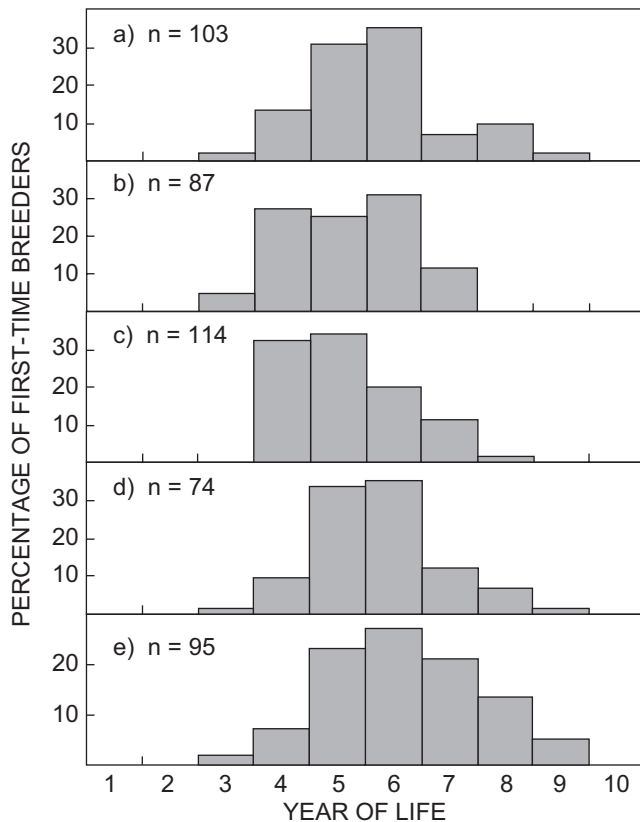


Figure 1: Age at first recorded breeding for birds banded as chicks at a) Bird Island, b) Robben Island, c) Dassen Island, d) Ichaboe Island and e) Mercury Island, all cohorts combined

Probability of breeding

At Robben and Dassen islands, where the most intensive monitoring took place, over 50% of banded birds were found breeding by the age of four (Table 5). By the age of six, all Robben Island birds and 98% of the Dassen Island birds had been recorded breeding. In contrast, at the other three colonies, 50% of banded birds were not found breeding until the age of five (Table 5). By the age of six, the proportions of banded birds breeding at these three colonies ranged from 81% to 92% and it was not until the age of eight that all had been found breeding.

Discussion

Monitoring effort is likely to have been a major contributory factor to the differences found in age of first recorded breeding between cohorts and colonies. The only colonies that did not differ significantly were the two that received the most regular and highest intensity of monitoring (Robben and Dassen islands). There was also no significant difference in age at first recorded breeding between cohorts at these two colonies. Monitoring effort was not uniform between colonies and was more intense in some years than in others. Also, breeding penguins are not equally visible at the different colonies. It is probably hardest to find those breeding at Dassen Island, where most nest in burrows, and at Robben Island, where they are obscured by thick bush.

This may have resulted in an over-estimate of age at first breeding in some instances due to earlier breeding attempts being unobserved. However, in spite of this, mean and median estimates of age at first breeding were lowest for these two colonies. The topography of Mercury Island made access to nesting birds in some areas difficult.

Birds banded in the earliest years of the study returned the greatest mean and median ages of first recorded breeding. This is to be expected, given that the maximum age at which a bird can be detected breeding for the first time decreases by a year with each cohort, because the period of observations is reduced by a year. However, it is also likely that monitoring intensity played a part in producing this distribution of first recorded breeding attempts.

Given the relatively high observer effort at Bird Island in 1994 and 1995, it might be expected that birds that were banded in 1992 would have been detected if they had attempted breeding before the end of their third year. The peak of first breeding records of 1992 birds in their seventh year and of 1994 birds in their fifth year can be explained by the large number of re-sightings made in 1999 (Figure 3a, Appendix 1). Another explanation for the late detection of breeding by birds banded in 1992 may be the relatively small sample size of birds banded as chicks in that year. The number banded in 1992 was only 13% of the total banded in 1994 and 11% of that banded in 1995 (Table 1). It may, therefore, have been more difficult to locate the relatively small number of birds from the 1992 cohort that returned to breed, even though the proportion found breeding was by far the highest for any cohort at any colony (Table 1).

At Robben Island, the findings from this study were similar to those of Crawford *et al.* (1999). The earliest recorded breeding of 66 known-age birds at Robben Island was one year and eight months (Crawford *et al.* 1999). However, the nest was abandoned within two weeks of its discovery and no further breeding attempts were made by the bird that year. By the age of six, 80% of all known-age birds were breeding, most (36%) making their first breeding attempt in their fifth year of life (Crawford *et al.* 1999). In this study, the earliest recorded breeding was at 2.5 years old, all known-age birds were breeding by the age of six and 25% made their first breeding attempt in their fifth year of life.

At Ichaboe Island, many of the birds banded in 1992 were first recorded breeding in 1997, which was not reflected by a particularly high monitoring effort (Figure 3d). In addition, only six months of data were available for that year. At Mercury Island, in spite of a high re-sighting rate in 1996 (Figure 3c), few birds bred for the first time in that year (Appendix 1). The number of penguins breeding at Mercury Island decreased sharply from 1992 to 1994 as a result of food scarcity brought about by unusual environmental conditions (Kemper *et al.* 2001). This probably caused birds of the 1992–1993 cohorts from Mercury Island to defer their age at first breeding. In the Benguela system, Cape Cormorants *Phalacrocorax capensis* and Swift Terns *Sterna bergii* similarly are thought to defer their age at first breeding when food is scarce (Crawford *et al.* 2001 and 2002). Elsewhere, other species of penguins may defer breeding in years of low food availability (e.g. Croxall and Rothery 1995).

Table 4: Numbers of African Penguins banded as chicks that were oiled, cleaned, released and subsequently discovered breeding at each of five breeding colonies. Abbreviations are those used in Table 1

Breeding colony	1992			1993			1994			1995			Total		
	Nba	NBr	%Br	Nba	NBr	%Br	Nba	NBr	%Br	Nba	NBr	%Br	Nba	NBr	%Br
Bird Island	0	0	–	0	0	–	0	0	–	2	1	50	2	1	50
Robben Island	5	2	40	2	1	50	0	0	–	0	0	–	7	3	43
Dassen Island	3	1	33	0	0	–	0	0	–	0	0	–	3	1	33
Ichaboe Island	0	0	–	1	0	0	0	0	–	0	0	–	1	0	0
Mercury Island	0	0	–	0	0	–	0	0	–	0	0	–	0	0	–
Total	8	3	38	3	1	33	0	0	–	2	1	50	13	5	38

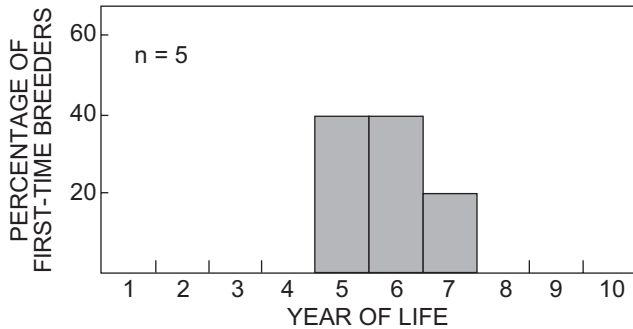


Figure 2: Age at first recorded breeding for birds banded as chicks and later oiled, cleaned and released. All years and colonies are combined

Table 5: Proportions (%) of birds banded as chicks between 1992 and 1995 that were breeding by ages between two and seven years old

Colony	Age (Years)						
	2	3	4	5	6	7	8
Robben Island	5	32	57	89	100	100	100
Dassen Island	0	32	67	87	98	100	100
Bird Island	2	16	47	82	88	98	100
Ichaboe Island	1	11	45	80	92	99	100
Mercury Island	2	9	33	60	81	95	100

Age at first breeding may vary between regions and between cohorts as a result of geographical and temporal variations in the energy cost of reproduction and available food resources. In southern Namibia there has been a significant decrease in the breeding African Penguin population and this is thought to be related to the contraction of the sardine population, due to overfishing (Cordes *et al.* 1999, Kemper *et al.* 2001). This paucity of food may be responsible for a delay in the age at which Namibian birds first attempted to breed.

Age at first recorded breeding of penguins that had been oiled, cleaned at the Southern African Foundation for Conservation of Coastal Birds (SANCCOB), and then released, did not differ significantly from that of birds that had not been oiled. This suggests that oiling, and subsequent treatment prior to release, did not offset the birds' first attempts to breed. However, it should be noted that the sample size of rehabilitated birds was only five.

The age at first breeding of 4–5 years old, evaluated for the African Penguin in this study, was similar to that

estimated by Randall (1983) at St Croix Island and by Crawford *et al.* (1999) at Robben Island. It also falls within the range of values estimated for other penguin species. Most Gentoo *Pygoscelis papua*, Yellow-eyed *Megadyptes antipodes* and Little Penguins *Eudyptula minor* breed for the first time when 2–3 years old (Richdale 1957, Dann and Cullen 1990, Marchant and Higgins 1990, Williams 1995). The youngest King and Emperor Penguins found breeding were three years old (Williams 1995). Adelie Penguins begin to breed when between four and seven years old (Ainley *et al.* 1983), Magellanic Penguins when 4 years old (PD Boersma *in litt.*) and Royal Penguins at five years old (Williams 1995). The mean age of first breeding estimated for African Penguins at Robben and Dassen islands in this study is similar to that found for the Magellanic Penguin, the only other member of the genus *Spheniscus* for which comparable data are available.

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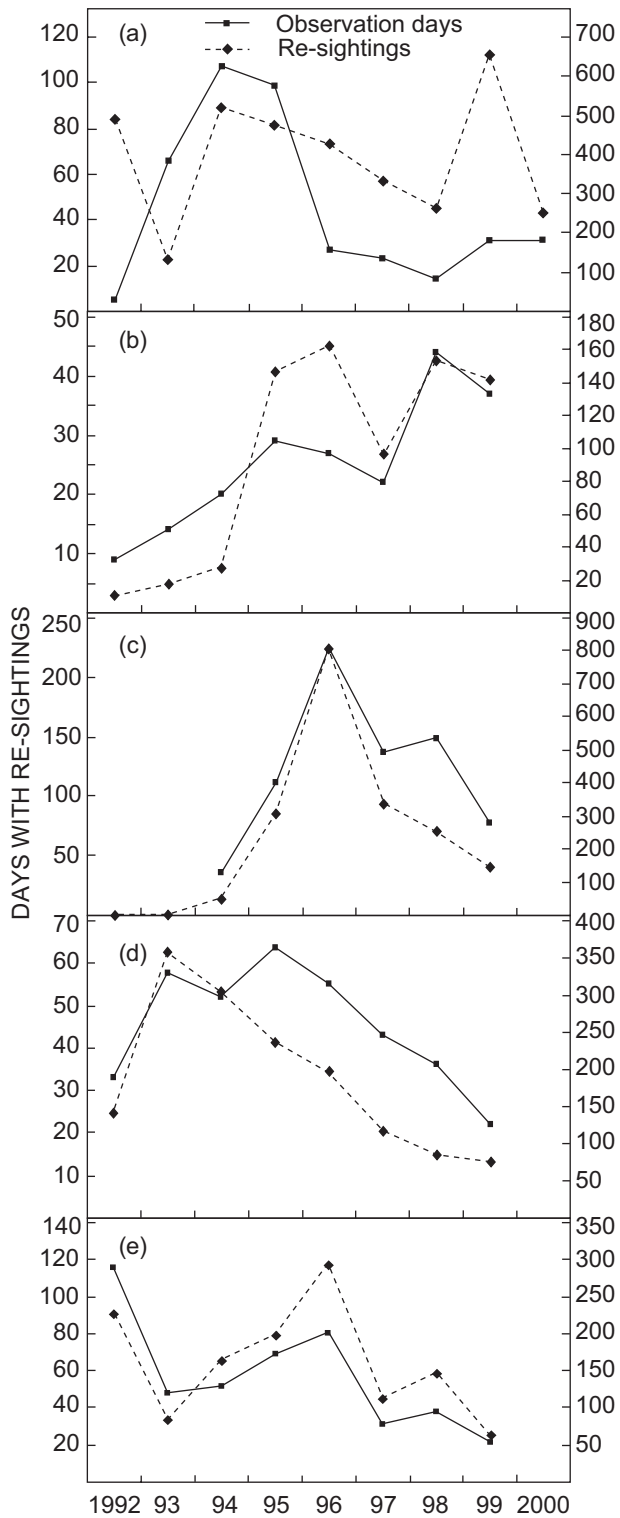


Figure 3: Numbers of days when re-sightings were made (Observation days) and total numbers of re-sightings made (Re-sightings) in each year at a) Bird Island b) Robben Island c) Dassen Island d) Ichaboe Island and e) Mercury Island

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Appendix 1: Proportions (%) of first-time breeders in each age class for 1992–1995 cohorts at five African Penguin colonies

Colony	Cohort	N	Year of Life						
			3	4	5	6	7	8	9
Bird Island	1992	14	7	7	7	21	29	14	14
	1994	36	3	0	47	22	6	22	0
	1995	53	0	25	26	47	2	0	0
Robben Island	1992	59	5	34	15	34	12	0	0
	1993	26	4	8	50	27	12	0	0
	1994	2	0	100	0	0	0	0	0
Dassen Island	1992	83	0	36	33	17	12	2	0
	1993	26	0	23	38	27	12	0	0
	1994	5	0	20	40	40	0	0	0
Ichaboe Island	1992	25	0	8	24	36	16	12	4
	1993	16	0	13	13	31	31	13	0
	1994	12	8	17	25	50	0	0	0
	1995	21	0	5	67	29	0	0	0
Mercury Island	1992	55	0	0	22	29	18	22	9
	1993	32	3	22	25	16	31	3	0
	1994	6	0	0	33	67	0	0	0
	1995	2	50	0	0	50	0	0	0